

NOTE

## Honeydew feeding in adult Noctuidae and Erebidae – some observations and a note on differing modes of access

Honeydew is the sugary excrement of various phloem sap feeding insects, particularly hemipterans, which is a major sugar source for many invertebrates (Stadler & Dixon, 2005; Wäckers, 2005). The attractiveness of honeydew to moths is long known (e.g. Wilkes, 1748-49). Nevertheless, published reports are sporadic (Pittioni, 1923; Johnson & Stafford, 1985; Leverton, 2001) and there is uncertainty over whether honeydew constitutes an important food source for adult Lepidoptera. Allan (1937) reckoned it to be the principal food of many species in the adult stage while more recently Johnson & Stafford (1985) concluded that they (excepting the Lycaenidae) probably 'rarely consumed' honeydew. Stoffolano (1995) considered the possibility that honeydew could be 'a major carbohydrate food source for adult lepidopterans' plausible but called on the need for evidence. Since then very considerable advances in understanding of mouthpart morphology, function and evolution in the Lepidoptera have been made and their relationship to feeding guilds elucidated (Petr & Stewart, 2004; Krenn, 2010; Zaspel *et al.*, 2011; Zenker *et al.*, 2011). For moths the focus of such work has fallen on fruit feeding, fruit piercing, skin piercing and lachryphagous genera – groups which hold a particular human interest or economic importance. Information on the adult feeding behaviour of many groups of nocturnal moths in general – and specifically about the use of honeydew – remains vague. Their honeydew feeding niche whilst perhaps not of economic importance is of significant ecological interest.

In published observations of moths found at honeydew in the British Isles which include details on the manner of feeding (many do not) most apparently

relate to honeydew which has fallen onto surfaces – typically upper leaf surfaces – beneath leaves or stems supporting aphids and is in a liquid state (e.g. Meldola, 1869; Leverton, 2001). I have been unable to find any reference to moths feeding at dried honeydew or interacting while foraging for honeydew with ants attending the producing aphid colony. References to the ingestion of honeydew by a moth directly from a producing aphid are rare (Esche, 1994; Steiner, 1994). The purpose of this note is to document instances of these behaviours and to put on record some observations which illustrate three distinct modes of moths (Lepidoptera: Noctuidae and Erebidae) winning access to the carbohydrate resource provided by aphids. All observations reported here were made in Hargate Forest in the High Weald 'Area of Outstanding Natural Beauty', UK (51°6' N, 0°14' E) in summer 2009. A secondary purpose of this note is to contribute to the documentation of those species of moth which feed on honeydew. As Corke (1999) remarks, even for the relatively species-poor and intensively observed British Rhopalocera fauna, data on which species use honeydew are limited; the same applies equally to macromoths.

On the night of 20th-21st June 2009 five species of noctuid were recorded feeding at honeydew on leaves of Stinging Nettle (*Urtica dioica* (Linnaeus)): *Noctua pronuba* (Linnaeus, 1758); *Diarsia mendica* (Fabricius, 1775); *Diarsia brunnea* (Denis & Schiffermüller, 1775); *Euplexia lucipara* (Linnaeus, 1758); *Apamea monoglypha* (Hufnagel, 1766). There were also individuals of *Hypena proboscidalis* Linnaeus, 1758 (Lepidoptera: Erebidae) and *Blastobasis lacticolella* Rebel 1940 (Lepidoptera: Blastobasidae) feeding. The moths were observed between 23:00 and 01:00. Large numbers of the Common Nettle Aphid (*Microlophium carnosum* Buckton, 1876), a species which is not attended by ants, were feeding from the stems of the plants. It was not a dewy evening, but many nettle leaf surfaces were coated with moist honeydew while others were only partially covered, the honeydewed areas being visible as glistening blotches. The whole of May and June had been relatively dry up to this point and there had been no significant rainfall in the preceding week during which the minimum-maximum temperature range was approximately 10°C

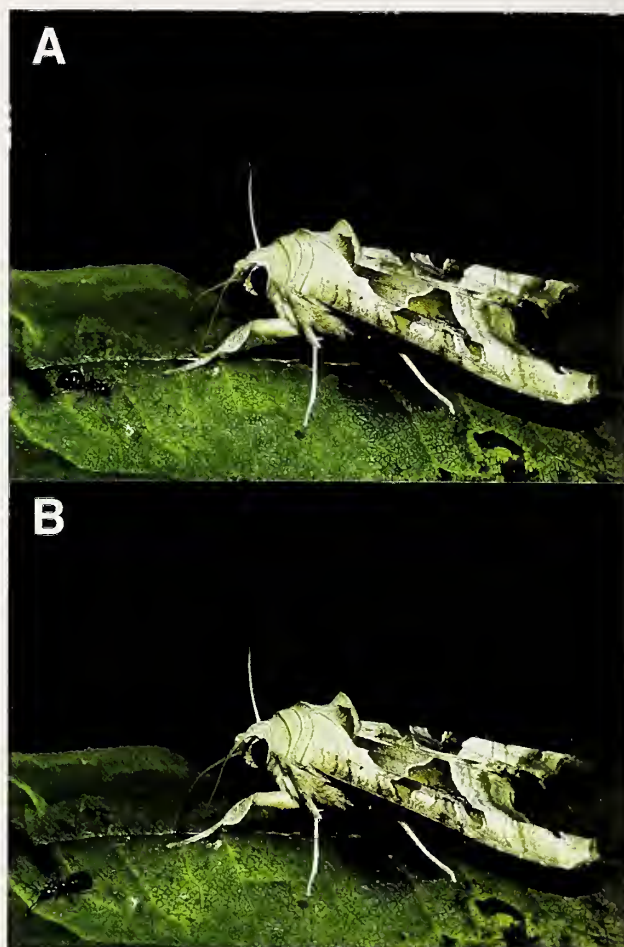
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to 22°C. The moths were active and alert and easily disturbed by the observer's approach. They regularly shifted their positions on the leaves or ran to other leaves, apparently 'foraging movements' to areas of greater moisture after a feeding patch became drained. During July, in eight subsequent visits to the same forest track, which had large stands of *U. dioica* along its ditches and verges, no moths were witnessed feeding at honeydew.

On the evening of 16th August between 23:00 and 00:00, at the same site, four other common noctuids were observed apparently feeding at honeydew from Rosebay Willowherb (*Chamaenerion angustifolium* (Linnaeus) Holub) leaves: *Ochropleura plecta* (Linnaeus, 1761); *Noctua janthe* (Borkhausen, 1792); *Xestia c-nigrum* (Linnaeus, 1758); *Phlogophora meticulosa* (Linnaeus, 1758). The plants in question were heavily populated by a species of *Aphis* (possibly *A. salicariae*) which formed colonies along the midribs on the leaf undersides. However, in this instance the upper leaf surfaces from which the moths fed – many of which were yellowing and curled at their margins – were all dry to the touch and without any visible moisture. The plants still had some flowers on them. These are known to be fed from by noctuid and geometrid moths (Leverton, 2001) but on this occasion no moths were observed visiting them. Both daytime and night-time temperatures had in general been higher than in June but with a similar lack of rainfall in the week or more before the observation. The temperature range in this week was approximately 14°C to 25°C.

It was possible to observe the *Phlogophora meticulosa* individual for a period of more than five minutes as it dabbed and swept a small area of surface near a leaf's midrib with the dorsal tip region of its bent proboscis. It did not move its legs and with the exception of the proboscis appeared quite motionless. The proboscis tip itself was sometimes raised momentarily but most of the time was in contact with the leaf along with the rest of the tip region. A sequence of photographs indicate that at least at one point the proboscis tip region became immersed in a small volume of liquid which had not been on the leaf surface nine seconds previously (Fig. 1). My interpretation is that this moth was discharging fluid in order to mobilise sugars dried onto the surface of the leaf before then imbibing this re-dissolved honeydew. The process whereby butterflies ingest nutrients from dry material using pulses of rapidly discharged and withdrawn saliva has been described by Downes (1973) and by Knopp and Krenn (2003). The other possibility is that the moth had accumulated minute particles of moisture from the leaf surface amongst the sensilla of its proboscis



**Figure 1.** *Phlogophora meticulosa* adult apparently accessing dried honeydew in the presence of an ant: a) shows proboscis with tip lifted after a period when the tip region was pressed flat against the leaf and repeatedly moved about within a small area of 1 or 2 cm<sup>2</sup> of leaf surface near the midrib; b) shows a small quantity of fluid at and around the area of contact between the proboscis tip region and leaf surface, the wetted part of the yellow proboscis having become translucent.

tip region and then deposited them as a consolidated droplet, but this seems unlikely given the obvious dryness of the leaf surface and the speed with which the fluid appeared.

As the moth fed the leaf was visited by a patrolling ant (*Lasius fuliginosus* (Latreille, 1798)). On approaching within a few millimetres of the moth's front tarsi and proboscis the ant turned away leaving the leaf surface and walked to another part of the plant. *Noctua janthe* and *Xestia c-nigrum* were noted to be present on separate leaf surfaces with the dorsal tip regions of their proboscises pressed into contact with the dry leaf surface and assumed also



to be feeding. No ants were seen to investigate these moths. *Ochropleura plecta* was seen in a similar habit on the surface of a *Rubus fruticosus* (Linnaeus) leaf underneath the same aphid colony where honeydew had evidently dripped.

Another species of moth, *Xestia xanthographa* (Denis & Schiffermüller 1775), was witnessed feeding on honeydew on *C. angustifolium* simultaneously but in a different way. This species was seen to run along the vertical stem of the plant and then dart out of sight beneath leaves. The action was rapid and difficult to follow; one needed to assume a position on the ground amongst the dense stand of *C. angustifolium* looking up at the undersides of the leaves but do so without jarring the plants so much that any moths present fell or flew away. This revealed a moth to be probing amongst the aphids attached to the midrib region of the leaf. Changes in position were achieved both by running along the midrib (the moth 'upside-down') and head and proboscis movements. These movements were repeatedly punctuated momentarily for two or three seconds while the dorsal tip region of the proboscis was held either in very close proximity to, or in tactile contact with, an aphid (Fig. 2). Figure 2 shows the dorsal tip region of the proboscis pressed against an aphid's abdomen, the tip itself about level with the siphunculi. Immediately after the photograph was taken (within five seconds) an ant approached urgently along the midrib from the direction of the leaf tip. The ant made contact with the tarsus of the moth's left front leg causing the moth to recoil its proboscis and move the leg to the leaf margin, repositioning itself with its head pointing upwards and towards the upper leaf surface. It was, however, reluctant to leave the aphid aggregation and remained in this position while the ant circled it making repeated runs at the moth's tarsi which it shifted in irritation but did not move away. This continued for between 30 seconds and a minute, after which the moth ran back to the main stem and onto the top of another leaf. After a short interval of about two minutes the same moth was observed foraging in the same way on the underside of another leaf with an aphid aggregation along its midrib.

The observations recorded here display three distinct approaches used by moths to obtain food from aphid honeydew. The first, whereby fluids are freely ingested from a wet surface or sometimes from patches of liquid honeydew on an otherwise dry leaf surface, is apparently as described by other observers of moths on *U. dioica* leaves (Greene, 1863; Meldola, 1869; Colthrup, 1916; Leverton, 2001). The potential importance of this particular sugar source (honeydew deposits on *U. dioica* leaves) to adult



**Figure 2** *Xestia xanthographa* adult with proboscis in tactile contact with an aphid on *Chamaenerion angustifolium* foliage apparently attempting to access honeydew direct from the producer. Shortly after the photograph was taken the moth's tarsus was attacked by an ant.

moths in the British Isles was first communicated by Greene (1880), who reported 37 species (including some geometrids and a pyralid as well as noctuids) using it. June appears to be the optimum time for this 'natural attraction' (although Greene does list a few late summer and autumn flying noctuids). In 2009 at my location conditions became wetter in late June and July, a possible explanation for the apparent cessation of honeydew feeding in July therefore being that honeydew deposits had been washed away by rain (Leverton, 2001). However, populations of *Microlophium carnosum* are known to peak in June anyway, and crash rapidly afterwards – probably owing to intraspecific competition and a deterioration in the food quality of the host plant (Perrin, 1976) – so the apparent correlation with weather conditions may be specious. The other common aphid species hosted by *U. dioica* in the British Isles, *Aphis urticae* (Gmelin, 1790), also forms dense colonies in spring and early summer, the species later aestivating as a population of small and dispersed individuals (Dixon, 1998).

The conditions stated for honeydew to be effective as a 'natural attraction' to moths in the British Isles are dewy (Collins, 1890-91; Tutt, 1902; Leverton, 2001) or foggy (Forsyth, 1890-91) evenings during dry or hot spells. In these periods of relative drought aphid populations are said to increase rapidly and the resulting excess of honeydew can accumulate on surfaces without being washed away by rainwater. Dew or damp night air on the other hand may soften or dissolve dried and crystallised honeydew deposits



(or dilute those that have become viscous through evaporation at the leaf surface) an implication being that this may render the carbohydrates more accessible to fluid feeding Lepidoptera (Merrifield, 1906; Leverton, 2001). However, since various butterflies utilise honeydew by day, including some species of the Lycaenidae for which it is the principal food source in the adult stage (Corke, 1999; Thomas, 2010), it follows that dew or other very particular meteorological conditions need not be absolutely necessary for uptake of honeydew by the lepidopteran proboscis. In the first case described here, since temperatures were not excessive in the week of the observation, the rainless conditions may have contributed to the build-up of honeydew deposits which were able to remain sufficiently moist by nightfall for Lepidoptera to easily access them.

Two months later however, in the second case, dried honeydew was apparently being used as a food source by four noctuid species. Stoffolano (1995) makes the point that while some adult lepidopterans are able to exploit nectars above optimal concentration or viscosity by using saliva to dilute them (for example *Autographa gamma* Linnaeus 1758; Proctor & Yeo, 1972) the question of whether Lepidoptera can detect, and subsequently process, dried honeydew does not seem to have been addressed. The observation here on *P. meticulosa* supports a belief that some noctuids can do so.

Although the question was raised as long ago as the 1840s (Logan, 1849), how moths detect honeydew (either in a dried or liquid state) does not seem to have been explained yet. Johnson and Stafford (1985) suggest that low apparency of both honeydew and its producers (relative to visually advertised floral nectars) may be a factor which limits lepidopteran access to honeydew. This interpretation does however seem to be founded on the visual (or partly so) foraging of diurnal Rhopalocera not on night-flying moths (which comprise the majority of lepidopteran species) which, as they do note, are evidently capable of locating sugar sources such as tree sap and artificial bait using other, presumably olfactory, stimuli. There are numerous historical, and anecdotal, examples of moths being preferentially attracted by honeydew over other, ostensibly more conspicuous, food sources, both natural and artificial (e.g. Logan, 1849; Woodforde, 1895). Norris (1936) placed honeydew into a class of foods which "can only be detected by their smell" and therefore, since the sugars themselves are not volatile, "are only attractive in a fermenting state." However, although alcohol is perhaps a candidate, the chemical identity of any volatiles emitted from honeydew which might function as a remote (i.e. while not in tarsal contact with the honeydew) attractant to nocturnal moths does not seem to have been determined, nor

the distance range of their detectability. In other insect orders honeydew has been shown to function as a kairomone, involved in prey or host location for various predators and parasitoids of hemipterans (e.g. Wäckers, 2000). Van Emden & Hagen (1976) showed that a breakdown product of tryptophan (an amino acid present in some honeydews) was attractive to a neuropteran aphid predator. Recently Leroy *et al.* (2011) have shown bacteria in honeydew to emit volatiles to which a dipteran aphid natural enemy responded. Aphids themselves can emit volatiles including, but not limited to, alarm pheromones (Francis *et al.*, 2005). There is therefore a possibility of honeydew food sources being located indirectly by the olfactory detection of their producers. These various semiochemical systems are as yet poorly understood but there are clearly a range of possible signal types that adult Lepidoptera might read in order to find honeydew for feeding purposes.

In the third case, *Xestia xanthographa*, appears to have imbibed honeydew directly from aphids. The observation was too brief to confirm if the moth actually stimulated the aphids to release honeydew but this seems probable. The moth's initial reluctance to retreat from the aphid aggregation and its rapid adoption of another one having been challenged by the ant suggests a behaviour more purposeful than the opportunistic gleaning of sugars. All the insects involved were 'upside-down'. Any unsolicited honeydew emissions would therefore have tended to fall away from the foraging site. Together with the fact that the aphid colony was apparently ant defended the simplest explanation for the moth's observed actions seems to be that it sought to capture the ants' honeydew harvest and that it possesses a suitable technique for doing this.

The behaviour of *Xestia xanthographa* described here may be analogous to that reported by Johnson and Stafford (1985) whereby two species (also Noctuids, *Aseptis characta* (Grote) and *Parabagrotis exsertistigma* (Morrison)) were observed feeding on aphid honeydew on *Artemisia tridentata* (Nuttall) in a canyon in Idaho, USA. These insects moved their proboscides from aphid to aphid in a way likened to 'locating composite inflorescences and probing individual florets' although it is not precisely clear from the report whether this was interpreted as active stimulation of honeydew secretion or just gleaning of excess honeydew from the aphids' feeding site.

Tactile stimulation of hemipterans, by the lepidopteran proboscis, to elicit honeydew excretion is known to occur but has not been widely reported. It is the main adult feeding strategy in some Asian Lycaenidae (subfamily Miletinae) (Fiedler, 1993). It

was also reported in 1928 that *Yponomeuta cognatella* (Hübner) (Yponomeutidae) in the course of 'prodding at leaves' would sometimes prod aphids with extended proboscis causing them to exude drops of honeydew (which were then consumed). However, these were captive insects and, at the time, the moths' stimulation of honeydew exudation was interpreted to be unintentional (Thorpe, cited in Norris, 1936 and Scoble, 1992). In the Atlantic forest of Costa Rica recently, a noctuid moth, *Elaeognatha argyritis* Hampson, was seen to tap the wings of a lantern bug (Fulgoroidea) not with its proboscis, but with its antennae, which resulted in the ejection of a honeydew stream then caught on the moth's partially extended proboscis (Naskrecki & Nishida, 2007).

Regardless of whether the behaviour of *X. xanthographa* described here can be construed as imitation of ant-aphid attendance it does show that moths are capable of locating and obtaining honeydew directly from aphids even in the presence of attending ants. Wäckers (2005) stated that "in heavily tended colonies honeydew is often not accessible to insects other than ants." In this instance it seems that ant attendance levels were high enough to impose some foraging risk on the *Xestia xanthographa* individual but insufficient to render the honeydew inaccessible to other insects (honeydew had accumulated on some leaf surfaces underneath aphid aggregations). Presumably the compensating advantage for the moth of this behaviour was the elimination of the cost of dealing with the problems of evaporation and crystallisation to which honeydew sugars are prone (Wäckers, 2000). In this respect the behaviour presents an interesting contrast with that of the *P. meticulosa* also described in this note.

Although honeydew may be unreliable as a 'natural attraction' this may belie its importance as a food source. Allan (1937, 1945) claimed that honeydew was the principal food of many Lepidoptera in the adult state, particularly woodland moths. Johnson and Stafford (1985) considered that the "paucity of observations on this behaviour" in non-lycaenid Lepidoptera could be due to the insects being "less conspicuous when feeding on honeydew than when feeding on nectar." Moreover, even though recent reports are not plentiful there are sufficient historical references to honeydew feeding in Europe to at least demonstrate that the habit cannot be rare (e.g. South, 1878; Barrett, 1893-1907; Scorer, 1913). The diversity of species recorded at honeydew by some observers (e.g. Pittioni, 1923; Dancy & Savage, 1945; Leverton, 2001) further supports the belief that this type of feeding behaviour is not untypical in nocturnal Lepidoptera, particularly in view of honeydew's ubiquity as a sugar source in many habitats (Wäckers, 2005).

The observations detailed in this note suggest that moths are capable of utilising honeydew as a carbohydrate source in varying circumstances and using a variety of foraging techniques – and not under any especially unusual ecological or environmental conditions. This further supports the notion that honeydew feeding in adult Lepidoptera may be more commonplace than the assumption of a predominantly nectar based diet, so often attached to general accounts of the Lepidoptera (e.g. Gullan & Cranston, 2010), indicates.

## LITERATURE CITED

- ALLAN, P.B.M. 1937. A moth-hunter's gossip. Watkins and Doncaster, London. 319 pp.
- ALLAN, P.B.M. [as An Old Moth-hunter] 1945. Honey-dew. Entomologist's Record and Journal of Variation 57: 93-97.
- BARRETT, C.G. 1893-1907. The Lepidoptera of the British Isles. 11 vols. Reeve and Co., London.
- COLLINS, J. 1890-91. Notes on *Xanthia cerago* and *X. silago*. Entomologist's Record and Journal of Variation 1: 68.
- COLTHRUP, C.W. 1916. Spiders attacking moths after dark. Entomologist's Record and Journal of Variation 28: 68.
- CORKE, D. 1999. Are honeydew/sap-feeding butterflies (Lepidoptera: Rhopalocera) affected by particulate air-pollution? Journal of Insect Conservation 3: 5-14.
- DANCY, T.A. & SAVAGE, L.E. 1945. Noctuae captures in Mid-Sussex from the Yew hedges. Entomologist's Record and Journal of Variation 57: 58-59.
- DIXON, A.F.G. 1998. Aphid ecology: an optimization approach. 2nd edition. Chapman and Hall, London. 300 pp.
- DOWNES, J.A. 1973. Lepidoptera feeding at puddle margins, dung, and carrion. Journal of the Lepidopterists' Society 27: 89-99.
- ESCHE, T. 1994. Aspekte zur Nahrungskonkurrenz unter Nachtfaulen. pp. 51-53. In: Ebert, G. (ed.), Die Schmetterlinge Baden-Württembergs, Vol. 3: Nachtfalter 1, E. Ulmer, Stuttgart.
- FIEDLER, K. 1993. The remarkable life history of two Malaysian lycaenid butterflies. Nature Malaysiana 18: 35-43.
- FORSYTH, A. 1890-91. Notes on *Xanthia cerago* and *X. silago*. Entomologist's Record and Journal of Variation 1: 68.
- FRANCIS, F., VANDERMOTEN, S., VERHEGGEN, F., LOGNAY, G. & HAUBRUGE, E.E. 2005. Is the (E)-beta-farnesene only volatile terpenoid in aphids? Journal of Applied Entomology 129: 6-11.
- GREENE, J. 1863. The insect hunter's companion. van Vootst, London. 164 pp.
- GREENE, J. 1880. The insect hunter's companion. 3rd Edition. Swan Sonnenschein & Allen, London. 114 pp.
- GULLAN, P.J. & CRANSTON, P.S. 2010. The insects: an outline of entomology. 4th Edition. Wiley, Chichester. 565 pp.
- JOHNSON, J.B. & STAFFORD, M.P. 1985. Adult Noctuidae feeding on honeydew and a discussion of honeydew feeding by adult Lepidoptera. Journal of the Lepidopterists' Society 39: 321-327.
- KRENN, H.W. 2010. Feeding mechanisms of adult Lepidoptera: structure, function, and evolution of the mouthparts. Annual Review of Entomology 55: 307-27.
- KNOPP, M.C.N. & KRENN, H.W. 2003. Efficiency of fruit juice feeding in *Morpho peleides* (Nymphalidae, Lepidoptera). Journal of Insect Behaviour 16: 67-77.
- LEVERTON, R. 2001. Enjoying moths. Poyser, London. 276 pp.
- LEROY, P.D., SABRI, A., HEUSKIN, S., THONART, P., LOGNAY, G., VERHEGGEN, F.J., FRANCIS, F., BROSTAU, Y., FELTON, G.W. & HAUBRUGE, E. 2011. Microorganisms from aphid honeydew attract and enhance the efficacy of natural enemies. Nature Communications 2: 348 available online: <http://dx.doi.org/10.1038/ncomms1347>



- LOGAN, R.F. 1849. Moths and honeydew. *The Zoologist* 7: 2626.
- MELDOLA, R. 1869. Noctuas on Stinging Nettles. *The Entomologist* 4: 303.
- MERRIFIELD, F. 1906. President's address. *Transactions of the Entomological Society of London* for 1906. cxiii-cxliii.
- NASKRECKIA, P. & NISHIDA, K. 2007. Novel trophobiotic interactions in lantern bugs (Insecta: Auchenorrhyncha: Fulgoridae). *Journal of Natural History* 41: 2397-2402.
- NORRIS, M. J. 1936. The feeding-habits of the adult Lepidoptera Heteroneura. *Transactions of the Royal Entomological Society of London* 85: 61-90.
- PERRIN, R.M. [1976]. The population dynamics of the stinging nettle aphid, *Microlophium carnosum* (Bukt.). *Ecological Entomology* 1: 31-40.
- PETR, D. & STEWART, K.W. 2004. Comparative morphology of sensilla styloconica on the proboscis of North American Nymphalidae and other selected taxa (Lepidoptera): systematic and ecological considerations. *Transactions of the American Entomological Society* 130: 293-409.
- PITTONI, B. 1923. Noctuidenfäng an "natürlichen" Köder. *Entomologische Zeitschrift* 37: 21-22.
- PROCTOR, M. & YEO, P. 1972. *The pollination of flowers*. Taplinger Publishing Co., New York. 418 pp.
- SCOBLE, M.J. 1992. *The Lepidoptera: form, function, and diversity*. Oxford, Oxford University Press. 416 pp.
- SCORER, A.G. 1913. *The entomologist's log-book*. Routledge, London. 374 pp.
- SOUTH, R. 1878. Sugar versus honeydew. *The Entomologist* 11, 271-272.
- STADLER, B. & DIXON, A.F.G. 2005. Ecology and Evolution of Aphid-Ant Interactions. *Annual Review of Ecology, Evolution, and Systematics* 36: 345-372.
- STEINER, A. 1994. Beobachtungen an natürlichen Nahrungsquellen. pp. 44-50. *In: Ebert, G. (ed.), Die Schmetterlinge Baden-Württembergs, Vol. 3: Nachtfalter 1*, E. Ulmer, Stuttgart.
- STOFFOLANO, J.G., JR. 1995. Regulation of a carbohydrate meal in the adult Diptera, Lepidoptera, and Hymenoptera. pp. 210-247. *In: de Boer, G. and R. F. Chapman (eds.), Regulatory mechanisms of insect feeding*. Chapman & Hall, New York. 398 pp.
- THOMAS, J. 2010. *Butterflies of Britain and Ireland*. British Wildlife Publishing, Dorset. 288 pp.
- TUTT, J. W. 1902. *Practical hints for field lepidopterists*. Volume II. Elliot Stock, London. 143 pp.
- VAN EMDEN H.F. & HAGEN, K.S. 1976. Olfactory reactions of green lacewing, *Chrysopa carnea*, to tryptophan and certain breakdown products (Neuroptera-Chrysopidae). *Environmental Entomology* 5: 469-473.
- WÄCKERS, F.L. 2000. Do oligosaccharides reduce the suitability of honeydew for predators and parasitoids? A further facet to the function of insect-synthesized honeydew sugars. *Oikos* 90: 197-201.
- WÄCKERS, F.L. 2005. Suitability of (extra-) floral nectar, pollen, and honeydew as insect food sources. pp. 17-74. *In: Wäckers, F.L., P.C.J. van Rijn, & J. Bruin (eds.), Plant-provided food for carnivorous insects: A protective mutualism and its applications*. Cambridge University Press, Cambridge. 356 pp.
- WILKES, B. 1748-49. *The English moths and butterflies*. London. 63 pp.
- WOODFORDE, F.C. 1895. Sugar versus natural food. *The Entomologist* 28: 264-266.
- ZASPEL, J.M., WELLER, S.J. & BRANHAM, M.A. 2011. A comparative survey of proboscis morphology and associated structures in fruit-piercing, tear-feeding, and blood-feeding moths in Calpinae (Lepidoptera: Erebidae). *Zoomorphology* 130: 203-255.
- ZENKER, M.M., PENZ, C., PARIS, M., & SPECHT, A. 2011. Proboscis morphology and its relationship to feeding habits in noctuid moths. *Journal of Insect Science* 11:42 available online: [insectscience.org/11.42](http://insectscience.org/11.42)

PHILIP SANSUM, [philip.sansum@gmail.com](mailto:philip.sansum@gmail.com)